

中国藓类植物无性繁殖体的初步观察^{*}

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摘要: 无性生殖在苔藓植物的生活史中起着重要的作用, 并且常通过各种无性繁殖体来完成。无性繁殖体的形态常被用来辅助鉴定一些不育的藓类植物。本文通过对 38 种藓类植物的无性繁殖体进行显微观察, 结果显示: 无性繁殖体在不同的藓类植物之间已经过多次演化; 无性繁殖体的形态在种内是相对稳定的, 且与其着生位置、配子体的分枝方式密切相关, 而与植物的系统位置以及生境并无直接的关系; 无性繁殖体的颜色与其胞壁的厚度以及表面纹饰密切相关。此外, 无性繁殖体的产生常常与假根、原丝体有共存关系。在研究中发现, 藓类植物的无性繁殖体主要包括原丝体芽胞、无性芽胞 (叶生芽胞、中肋芽胞、枝生芽胞)、芽体、假根芽胞和假根状块茎; 其中原丝体芽胞和无性芽胞最为常见。

关键词: 藓类植物; 无性繁殖体; 原丝体芽胞; 芽胞; 芽体; 假根芽胞; 假根状块茎

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Observations on the Asexual Diaspores of Mosses in China

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Abstract: Asexual reproduction plays an important role in the life cycle of bryophytes. Usually, mosses complete their asexual reproduction by different diaspores. The morphology of asexual diaspore has been commonly used for delimiting sterile mosses. In the present paper, asexual diaspores of 38 gemmiferous mosses were observed under light microscope. The results showed that the asexual diaspores have evolved several times independently in different moss lineages. The morphology of asexual diaspore is generally stable within species, and is closely related to its growing position and branching mode of gametophyte, but not to phylogenetic positions of the plants and their habitats. The color of diaspore is determined by the thickness of the diaspore wall and its ornamentation on the surface. In addition, the asexual diaspores often coexist with rhizoids or protonemata. In this study, asexual diaspores include protonemal gemmae and gemmae (laminar gemmae, costal gemmae, stem gemmae), bulbils, rhizoidal tubers and rhizoidal gemmae. Among them, protonemal gemmae and gemmae are the commonest asexual diaspores.

Key words: Asexual diaspores; Bulbils; Gemmae; Mosses; Protonemal gemmae; Rhizoidal gemmae; Rhizoidal tubers

Asexual reproduction plays an important role in the life cycle of bryophytes. It is predominant in the bryophytes especially when plants are under extremely hostile conditions (Jia,

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1994). In mosses, asexual reproduction is completed by various diaspores, including caducous shoot apices, caducous branchlets, flagelliform shoots, bulbils, caducous leaves, caducous leaf apex, fragile leaves, rhizoidal tubers and gemmae (Imura and Iwatsuki, 1990; Newton and Mishler, 1994; Imura, 1994; Laaka-Lindberg *et al.*, 2003). In some genera, e. g., *Bryum*, *Campylopus*, and *Pohlia*, asexual diaspores were used as one of the diagnostic characters for specific identification (Crundwell and Nyholm, 1964; Syed, 1973; Smith, 1978; Mohamed, 1979; Shaw, 1981; Sloover and Szmaida, 1981; Flowers, 1983; Cetin, 1999; Ashton and Raju, 2001; Sherock and Shaw, 2005).

Due to its great variability of topography and climate, China boasts a rich moss flora of having ca. 16% moss species of the world (Redfearn *et al.*, 1996). Thus, the knowledge of diaspores of Chinese moss flora is important to better understand the systematic relationships among the bryophyte groups. The asexual diaspores of mosses in China, however, have not been comprehensively investigated, and the terminology for describing them is not standardized and sometimes confusing. For example, the asexual diaspores of Chinese mosses were not specified and were called as gemmae except for the flagelliform branches in some Chinese literatures (Gao, 1994, 1996; Hu and Wang, 2005; Li, 2000, 2006; Wu and Jia, 2004; Wu, 2002). Another example is that the bulbils, commonly referring to the diaspore of *Brachymenium exile* by some authors (Smith, 1978; Lonton and Schuster, 1983; Reese, 1984) were also called as gemmae by Li (2006).

In the present study, 38 gemmiferous mosses representing 12 families and 27 genera from China were examined under the light microscope (LM). Our aims are 1) to describe the gross morphology of asexual diaspores found in some Chinese mosses, and to classify the asexual diaspores into types according to their growing po-

sition and development; 2) to recognize various factors that affect the characters of asexual diaspores in mosses; 3) to determine the significance of diaspore characters in taxonomy and systematic evolution. The terms concerning asexual diaspores follow Imura and Iwatsuki (1990) and Newton and Mishler (1994).

Materials and methods

Thirty-eight gemmiferous specimens were thoroughly cleaned through a series of rinses and mounted in water (Duckett and Pressel, 2003) and photographed with a digital camera under OLYMPUS CX 31 light microscopes (LM). Vouchers (Table 1) are deposited in the following herbaria: herbarium of the Institute of Botany, Chinese Academy of Sciences, Beijing (PE), herbarium of Kunming Institute of Botany, Chinese Academy of Sciences (KUN), and herbarium of East China Normal University (HSNU).

Classification of asexual diaspores

Characters of the asexual diaspores in the 38 species of gemmiferous mosses observed in the present study are summarized in Table 1.

According to the origin of the asexual diaspores, Newton and Mishler (1994) recognized that the asexual diaspores may come primarily from the asexual spores, protonema, rhizoids, shoots, leaves, modified protonema and gametophyte. In this study, asexual diaspores include protonemal gemmae (from protonema), rhizoidal tuber and rhizoidal gemmae (from rhizoids), bulbils (from shoots), and gemmae (from modified protonema). Among them, protonemal gemmae and gemmae are the commonest types of diaspores.

1. Protonemal gemmae

Protonemal gemmae usually formed on the protonemata which occur in leaf axil. Their shapes are diverse, including filamentous (*Tortula schmidii*, Plate I : 6), clavate (*Leptodontium flexifolium*, Plate I : 8) and spherical (*Barbula coreensis*, Plate I : 11–12).

2. Modified protonema-gemmae s. s. (probably representing a regenerating protonema in a state of arrested development)

Gemmae are specialized organs serving as asexual reproduction. The gemmae observed were classified into the following three categories based on developmental origin: laminar gemmae, costal gemmae and stem gemmae.

1) Laminar gemmae

Laminar gemmae are usually clavate or fusiform, originated from leaf cells, e. g., in *Plagiothecium latebricola* (Plate III : 34) and *Hookeria acutifolia* (Plate III : 31–32).

2) Costal gemmae

Costal gemmae are usually clavate or filamentous, and derived from costa cells. They can be produced on the costa at the leaf apex, middle or base, on ventral or dorsal side, e. g., in *Syrhophodon parasiticus* (Plate I : 1–2) and *Mitthyridium fasciculatum* (Plate I : 4).

3) Stem gemmae

Stem gemmae often occur on stems or short branches, deriving from cortical cells. They may be clavate or filamentous, e. g., in *Clastobryopsis planula* (Plate III : 36) and *Trachyloma indicum* (Plate II : 28).

3. Bulbils

Bulbils are highly condensed, vermicular or bud-like structures, with leaf primordial found in leaf axil of some mosses (Newton and Mishler, 1994). It is regarded as an extremely reduced branch (Imura and Iwatsuki, 1990). Two kinds of shapes are found in this type of diaspore; bulk-like bodies (e. g., in *Brachymerium exile*, Plate II : 20) and vermicular ones (e. g., in *Pohlia prolifera*, Plate II : 19).

4. Rhizoidal tubers

Rhizoidal tubers are defined as asexual organs occurring on the rhizoids, often spherical to ellipsoidal, pyriform, or occasionally tuberous, thick-walled, reddish brown to dark brown (Whitehouse, 1966), e. g., in *Bryum bornholmense* (Plate II : 22).

5. Rhizoidal gemmae

Rhizoidal gemmae are often filamentous, branched, or clavate, thick-walled and dark colored, originated directly from rhizoids, e. g., in *Rhizomnium tuomikoskii* (Plate II : 26).

Discussion

The majority mosses with asexual diaspores in this study are dioicous or sterile as previously noted (Longton, 1997; Imura and Iwatsuki, 1990). This suggests that asexual diaspores are found more frequently in dioicous or sterile mosses to compensate for sexual reproduction (Imura, 1994).

The characters of asexual diaspores are stable within each species, but not directly related

to the systematic positions and habitats of the plants. For example, the gemmae of *Hookeria acutifolia* are similar to those of *Plagiothecium latebricola* in morphology, but the two species are not closely related and with different habitats. For this reason, it is clear that the asexual diaspores have evolved several times independently in the different mosses lineages (Whitehouse, 1966).

The origin of diaspores was often used for classifying the asexual diaspores (Goebel, 1905; Newton and Mishler, 1994). In present study, we found that the characters of asexual diaspores are often depended on their growing positions on the plants. For example, the morphology of the costal gemmae are fairly uniform, such as clavate to filamentous, yellowish brown and thin-walled. In addition, the asexual diaspores for some species are affected by special environmental conditions or different ontogenetic phases. For example, in *Barbula horrinervis* (Plate I : 13), the acanthoid structure is produced by the germination of diaspores. Moreover, the diaspores of *Pohlia flexuosa* are often ovate in the early stage of development, but vermicular in the later one (Li, 2006). Only the ovate diaspores were observed in our study (Plate II : 18).

The branching modes of gametophyte play an important role in asexual reproduction (Jia, 1994). In this study, the asexual diaspores in acrocarpus mosses are produced on any parts of gametophyte, and their morphological characters are also varied. However, in pleurocarpus mosses, the asexual diaspores, only occurring on stems, protonemata or leaves, are often linear or clavate, yellowish brown.

The colors of asexual diaspores are mainly determined by the combination of wall pigmentation and copious quantities of yellow to brown lipid droplets within their cells (Imura and Iwatsuki, 1990; Duckett and Pressel, 2003). Moreover, the colors of asexual diaspores are often

depended on thickness of diasporal walls and its ornamentation on the surface. The thick-walled diaspores are often reddish brown or yellowish brown, verruculose or convex on the surface, but the thin-walled ones are light yellow, hyaline and smooth on the surface.

Rhizoids or protonema are usually produced on leaves, costae or the bases of plants as the asexual diaspores. The protonema are often irregularly branched or stalk-like, yellowish brown, and occur on the leaf axil, e. g. , in *Barbula indica* (Plate II : 16). The rhizoids, however, often occur on the leaf apice, costae or the bases of plants. The rhizoids on the leaf apex and costa are similar to normal ones in morphology, e. g. , in *Hookeria acutifolia* and *Mitthyridium fasciculatum*. Whereas, the rhizoids on the base of plants are usually irregularly branched, verruculose on the surface, e. g. , in *Bryum bornholmense* and *Pohlia lutescens*. It is note worthy that the asexual diaspores on the upper part of stem rarely coexist with rhizoids or protonema, but directly cluster on stems, e. g. , in *Clastobryopsis planula*.

Mostly, mosses complete asexual reproduction by a single type of diaspore. Only a few of mosses produce two or more types of diaspores (Whitehouse, 1966). In present study, two types of gemmae occur on different positions in *Bryum capillare*. One type of gemmae occurs on the yellowish brown, tuberculate, underground rhizoids. The gemmae are often deciduous, multicellular, pyriform to nearly spherical, reddish brown, with thick and smooth walls, and they are usually inflated, ca. 100—120 μm long, 65—70 μm wide. The second type grows on the stem near the leaf axil. The gemmae are uniseriate (up to 25 cells), linear, yellowish brown, thick-walled, verruculose on surface, and ca. 1.1 mm long.

References:

- Ashton NW, Raju VS, 2001. Development and germination of rhizoidal gemmae of *Bryum violaceum* [J]. *Cryptogamie Bryologie*, **22** (1): 3—11
- Chen PC (陈邦杰), 1963. Genera Muscorum Sinicorum (Pars Prima, in Chinese) [M]. Beijing: Science Press
- Chen PC (陈邦杰), 1978. Genera Muscorum Sinicorum (Pars Secunda, in Chinese) [M]. Beijing: Science Press
- Cetin B, 1999. *Barbula glauca* (Ryan) Möll., a new record for the moss flora of Turkey [J]. *Turkish Journal of Botany*, **23**: 69—70
- Crundwell AC, Nyholm E, 1964. The European species of the *Bryum erythrocarpum* complex [J]. *Transactions of the British Bryological Society*, **4**: 597—637
- Duckett JG, Pressel S, 2003. Studies of protonemal morphogenesis in mosses. IX. *Discelium nudum*: exquisite pioneer of unstable clay banks [J]. *Journal of Bryology*, **25**: 241—245
- Flowers S, 1983. Brood branches in *Philonotis* [J]. *The Bryologist*, **38**: 8—9
- Gao C (高谦), 1994. Flora Bryophytorum Sinicorum (in Chinese) [M]. Beijing: Science Press, **Vol. 1**: 1—368
- Gao C (高谦), 1996. Flora Bryophytorum Sinicorum (in Chinese) [M]. Beijing: Science Press, **Vol. 2**: 1—293
- Goebel K, 1905. Organography of plants. Part II, Special organography [M]. Oxford: Clarendon Press
- Hu RL (胡人亮), Wang YF (王幼芳), 2005. Flora Bryophytorum Sinicorum (in Chinese) [M]. Beijing: Science Press, **Vol. 7**: 1—287
- Imura S, Iwatsuki Z, 1990. Classification of vegetative diaspores on Japanese mosses [J]. *Hikobia*, **10**: 435—443
- Imura S, 1994. Vegetative diaspores in Japanese mosses [J]. *Journal of the Hattori Botanical Laboratory*, **77**: 177—232
- Jia Y (贾渝), 1994. A brief introduction of reproductive biology of bryophytes [J]. *Chenia* (隐花植物生物学), **2**: 1—14
- Laaka-Lindberg S, Korpelainen H, Pohjamo M, 2003. Dispersal of asexual propagules in bryophytes [J]. *Journal of the Hattori Botanical Laboratory*, **93**: 319—330
- Li XJ (黎兴江), 2000. Flora Bryophytorum Sinicorum (in Chinese) [M]. Beijing: Science Press, **Vol. 3**: 1—157
- Li XJ (黎兴江), 2006. Flora Bryophytorum Sinicorum (in Chinese) [M]. Beijing: Science Press, **Vol. 4**: 1—263
- Longton RE, Schuster RM, 1983. Reproductive Biology [A]. In: Schuster RM ed. New Manual of Bryology [M]. Nichinan: The Hattori Botanical Laboratory, **Vol. 1**: 386—462
- Longton RE, 1997. Reproductive biology and life-history strategies [J]. *Advances in Bryology*, **6**: 65—101
- Mohamed MAH, 1979. A taxonomic study of *Bryum billardieri* Schwaegr. and related species [J]. *Journal of Bryology*, **10**: 401—465
- Newton AE, Mishler BD, 1994. The evolution significance of asexual reproduction in mosses [J]. *Journal of the Hattori Botanical Laboratory*, **76**: 127—145
- Redfearn PL, Tan BC, He S, 1996. A newly updated and annotated checklist of Chinese mosses [J]. *Journal of the Hattori*

Botanical Laboratory, **79**: 63—357

- Reese WD, 1984. Mosses of Gulf South [M]. Baton Rouge: Louisiana State University Press
- Shaw AJ, 1981. A taxonomic revision of the propaguliferous species of *Pohlia* in North America [J]. *Journal of the Hattori Botanical Laboratory*, **50**: 1—81
- Sherock JR, Shaw AJ, 2005. *Pohlia robertsonii* and *P. rabauldensis* (Bryopsida, Mniaceae), two new species from the western and eastern and eastern United States [J]. *The Bryologist*, **108** (2): 177—182
- Sloover JL, Szmajda P, 1981. Propagules gemmiformes et propagules rameaux chez des *Campylopus africanus* [J]. *Bulletin du Jardin Botanique National de Belgique*, **51**: 213—218
- Smith AJE, 1978. The moss Flora of Britain and Ireland [M]. Cambridge: Cambridge University Press
- Syed H, 1973. A taxonomic study of *Bryum capillare* Hedw. and related species [J]. *Journal of Bryology*, **7**: 265—326
- Whitehouse HLK, 1966. The occurrence of tubers in European mosses [J]. *Transactions of the British Bryological Society*, **5**: 103—116
- Wu PC (吴鹏程), 2002. Flora Bryophytorum Sinicorum (in Chinese) [M]. Beijing: Science Press, **Vol. 6**: 1—290
- Wu PC (吴鹏程), Jia Y (贾渝), 2004. Flora Bryophytorum Sinicorum (in Chinese) [M]. Beijing: Science Press, **Vol. 8**: 1—482

Explanation of Plate

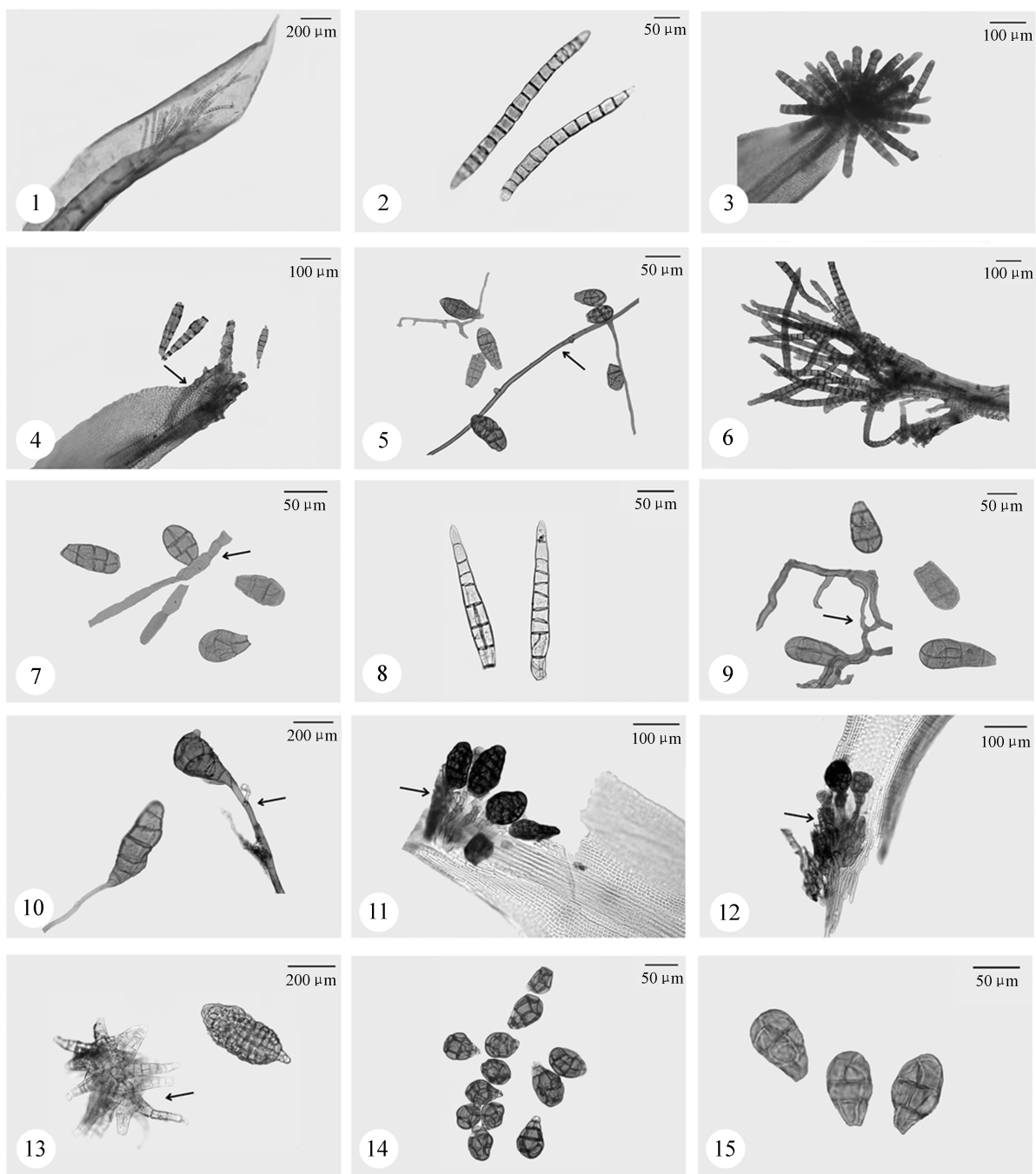
Plate I 1—9. Costal gemmae and protonemal gemmae 1, 2. Costal gemmae of *Syrrhopodon parasiticus*; 3. Costal gemmae of *Calymperes afzelii*; 4. Costal gemmae of *Mitthyridium fasciculatum*, showing rhizoids (at arrow); 5. Protonemal gemmae of *Anoetangium fauriei*, showing protonemata (at arrow); 6. Protonemal gemmae of *Tortula schmidii*; 7. Protonemal gemmae of *Desmatodon gemmascens*, showing protonemata (at arrow); 8. Protonemal gemmae of *Leptodontium flexifolium*; 9.

Protonemal gemmae of *Didymodon rigidulus*, showing protonemata (at arrow). 10—15. Protonemal gemmae and Rhizoidal tubers 10. Protonemal gemmae of *Didymodon ferrugineus*; 11, 12. Protonemal gemmae of *Barbula coreensis*, showing protonemata (at arrow); 13. Protonemal gemmae of *Barbula horneri*, showing germinated gemmae (at arrow); 14. Protonemal gemmae of *Barbula amplexifolia*; 15. Protonemal gemmae of *Timmiella anomala*

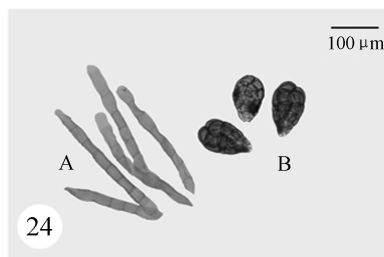
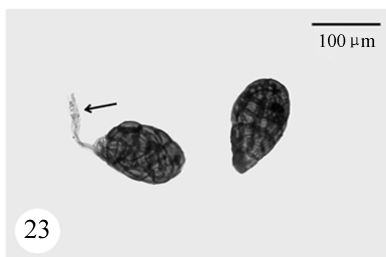
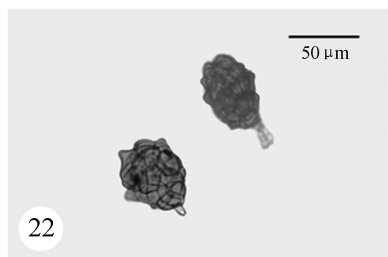
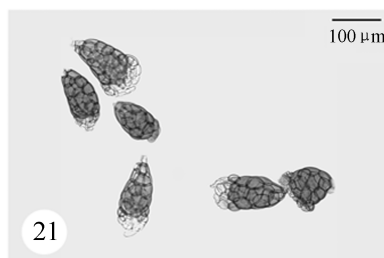
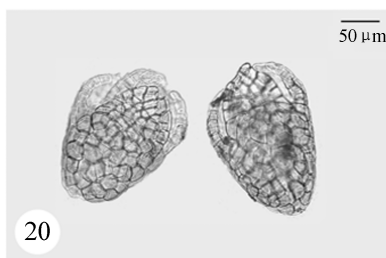
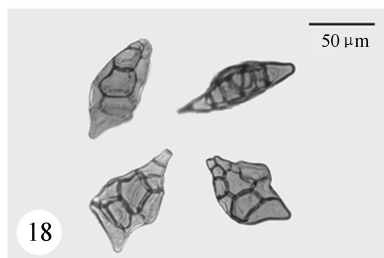
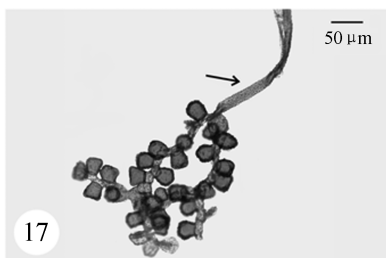
Plate II 16—18. Protonemal gemmae and Rhizoidal tubers 16. Protonemal gemmae of *Barbula indica*; 17. Rhizoidal tubers of *Pohlia lutescens*, showing rhizoids (at arrow); 18. Protonemal gemmae of *Pohlia flexuosa*. 19—27. Protonemal gemmae, bulbils, rhizoidal tubers, stem gemmae and rhizoidal gemmae 19. Bulbils of *Pohlia prolifera*; 20. Bulbils of *Brachymenium exile*; 21. Bulbils of *Bryum gemmigerum*; 22. Rhizoidal tubers of *Bryum bornholmense*; 23. Rhizoidal tubers of *Bryum thomsonii*, showing rhizoids (at arrow); 24. Rhizoidal tubers and stem gemmae of *Bryum capillare* (A shows stem gemmae, B shows rhizoidal tubers); 25. Stem gemmae of *Bryum tortifolium*; 26. Rhizoidal gemmae of *Rhizomnium tuomikoskii*; 27. Protonemal gemmae of *Rhachithecium perpusillum*, showing protonemata (at arrow). 28—30. Protonemal gemmae, laminar gemmae and stem gemmae 28. Stem gemmae of *Trachyloma indicum*; 29. Protonemal gemmae of *Pterobryopsis orientalis*; 30. Protonemal gemmae of *Horikawaea nitida*

Plate III 31—36. Protonemal gemmae, laminar gemmae and stem gemmae 31, 32. Laminar gemmae of *Hookeria acutifolia*, showing rhizoids (at 32); 33. Protonemal gemmae of *Cyathophorella hookeriana*; 34. Laminar gemmae of *Plagiothecium latebricola*, showing rhizoids (at arrow); 35. Stem gemmae of *Pylaisiadelphus yokohamae*; 36. Stem gemmae of *Clastobryopsis planula*. 37—42. Stem gemmae and bulbils 37. Stem gemmae of *Clastobryopsis robusta*; 38. Stem gemmae of *Clastobryum glabrescens*; 39. Stem gemmae of *Gammiella tonkinensis*; 40. Bulbils of *Pseudotaxiphyllum pohliaecarpum*; 41, 42. Stem gemmae of *Isopterygium propaguliferum*

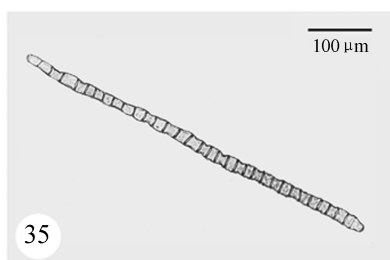
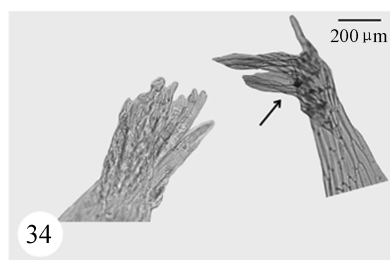
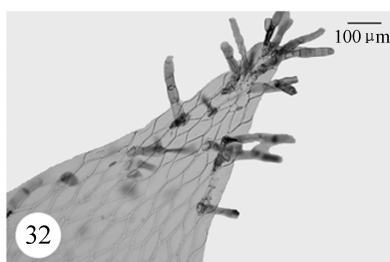
裴林英等：图版 I

PEI Lin-Ying *et al.*: Plate I

裴林英等：图版 II

PEI Lin-Ying *et al.*: Plate II

裴林英等：图版Ⅲ

PEI Lin-Ying *et al.*: Plate III